Wild vervet monkeys copy alternative methods for opening an artificial fruit

van de Waal, Erica ; Claidière, Nicolas ; Whiten, Andrew

DOI: https://doi.org/10.1007/s10071-014-0830-4

Originally published at:
van de Waal, Erica; Claidière, Nicolas; Whiten, Andrew (2015). Wild vervet monkeys copy alternative methods for opening an artificial fruit. Animal Cognition, 18(3):617-627.
DOI: https://doi.org/10.1007/s10071-014-0830-4

Wild vervet monkeys copy alternative methods for opening an artificial fruit

Erica van de Waal [a,b], Nicolas Claidière [c], Andrew Whiten [a,b*]

[a] Centre for Social Learning and Cognitive Evolution, and Scottish Primate Research Group, University of St Andrews, School of Psychology & Neuroscience, St Andrews, U.K.

[b] Inkawu Vervet Project, Mawana Game Reserve, Swart Mfolozi, KwaZulu Natal, South Africa

[c] Aix Marseille Université, CNRS, LPC UMR 7290, 13331, Marseille, France

[*] To whom correspondence should be addressed. E-mail: a.whiten@st-andrews.ac.uk

Corresponding author:

Andrew Whiten

University of St Andrews

School of Psychology & Neuroscience,

South Street,

St Andrews,

KY16 9JP, UK

Tel: 0044 1334 462073

ABSTRACT

Experimental studies of animal social learning in the wild remain rare, especially those that employ the most diagnostic tests in which alternative means to complete naturalistic tasks are seeded in different groups. We applied this approach to wild vervet monkeys (*Chlorocebus aethiops*) using an artificial fruit ('vervetable') opened by either lifting a door panel or sliding it left or right. In one group a trained model lifted the door and in two others the model slid it either left or right. Members of each group then watched their model before being given access to multiple baited vervetables with all opening techniques possible. Monkeys displayed a significant tendency to use the seeded technique on their first opening and over the course of the experiment. The option preferred in all 13 monkey's first successful manipulation session was highly correlated with the proportional frequency of that option they had previously witnessed. The social learning effects thus documented are not consistent with stimulus enhancement insofar as the same door knob was grasped for either technique. Results thus suggest that through imitation, emulation or both, new foraging techniques will spread across groups of wild vervet monkeys and potentially create foraging traditions.

Keywords: field experiments, social learning, imitation, cultural transmission, primates, vervet monkeys

INTRODUCTION

Social learning, traditions and cultural transmission in primates and other animals have received much attention in recent years (Hoppitt and Laland 2008; Kendal et al. 2010a; Whiten et al. 2011; Nielsen et al. 2012). A key methodological advance in the identification of social learning and dissection of the alternative processes underlying it occurred with the development of the 'two-action' method, in which experimental subjects witness a model proficient in using either of two different actions to manipulate an object such as an 'artificial fruit' (Whiten et al. 1996) and extract a reward from it. If subjects are subsequently more likely to match the alternative they witnessed in their own attempts at the task, we obtain evidence not only of the operation of social learning per se, but also some details of what is learned, as entailed by the differences in the witnessed alternatives that subjects subsequently match. After being first used by Dawson and Foss (1965), the two-action method has been employed effectively in numerous studies to identify the social learning of alternative actions such as the use of foot or beak to operate a foraging device by pigeons (Zentall et al. 1996); or blue tits' piercing or flipping a foil to access a reward (Aplin et al. 2013); alternative techniques to open artificial food objects by marmosets (Bugnyar and Huber 1997; Voelkl and Huber 2000) and alternative sequences of constituent behavioural elements by chimpanzees (Whiten 1998).

Such two-action studies have typically been dyadic, particularly in the early years of the approach, with an isolated subject learning from a single trained conspecific (Zentall 2012). More recently, the two-action concept has been enlisted in the design of experiments where the interest is in the social transmission and spread of action patterns in groups and broader populations

(Galef and Allen 1995). Among primates, such spread has been shown to occur with substantial fidelity in captive groups of capuchin monkeys (Dindo et al. 2008, 2009), chimpanzees (Whiten et al. 2005, 2007; Hopper et al. 2007) and vervet monkeys (van de Waal and Whiten 2012; van de Waal et al. 2013a).

Such studies remain rare in the wild (Whiten and Mesoudi 2008; Thornton and Clutton-Brock 2011), where they are inherently more difficult to engineer because there is less scope to control what an observer monkey witnesses. For primates, such experiments have been conducted recently in research by Kendal et al. (2010b), van de Waal et al. (2010), van de Waal and Bshary (2011), Schnoell and Fichtel (2012) and Gunhold et al. (2014a, 2014b). In the van de Waal studies, boxes acting as 'artificial fruits' were presented to wild vervet monkeys. A door at one end of the box could be opened by lifting it and a differently coloured door at the other end could be opened by sliding it, to obtain food inside. These two alternatives were seeded in different groups by initially locking the box so that only one opening technique could be used, until one dominant individual mastered it. Then both methods were made available to the rest of the group. This study demonstrated social learning from the initial model, but only when the model was a female monkey and not when it was the dominant male. However, because the different actions were modeled on different doors on the two ends of the box, the results may have reflected only local enhancement (Thorpe 1963), where the observer is simply more likely to focus their efforts on the side of the box that the model was manipulating.

To test for social learning that goes beyond local enhancement, and instead requires matching to what a subject witnessed either by imitation (defined by Whiten and Ham (1992) as 'learning

some aspect(s) of the intrinsic form of an act' from another individual) or emulation (replicating only the results of what the subject witnessed, such as the movements of parts of the object manipulated: Wood 1989; Tomasello 1990), we used the 'artificial fruit' (Whiten et al. 1996) we have dubbed a 'vervetable' and already employed successfully in studies with captive vervet monkeys, who discriminated and tended to copy whichever option they had witnessed (van de Waal et al. 2013a). The vervetable incorporates a single door that affords opening through alternative means, all of which involve contact with the same locus (a small knob in the centre of the door) such that local enhancement cannot explain any matching behaviour recorded. The door can be slid to either side, or alternatively lifted up, to gain access to the food reward inside. We seeded each of the different techniques (slide left, slide right or lift) in one adult female in each of three wild groups and investigated whether there was evidence for social learning of these alternative techniques by other group members, which would thus implicate emulation or imitation, and hence go beyond the findings of local enhancement found in wild vervet monkeys (van de Waal et al. 2010; van de Waal and Bshary 2011). We also tested whether the proportion of either of the two techniques that individuals observed being performed by any or all other successful group members (i.e. not only the model demonstrations) predicted the technique first used, as well as that preferentially employed over the whole experimental set-up. Such a correlation was reported by Perry (2009) in relation to white-fronted capuchins (*Cebus capucinus*) adopting whichever of two methods of natural fruit processing they had observed most; here, we address this question for the two techniques experimentally seeded in the groups studied.

METHODS

Study animals

Experiments were conducted by EW, with the help in each experiment of one of several staff members of the Inkawu Vervet Project (IVP), between 26 April 2012 and 3 October 2013 on three groups of wild vervet monkeys (*Chlorocebus aethiops*). All three groups ('Ankhase' (AK), 'Baie Dankie' (BD) and 'Noha' (NH)) are part of the Inkawu Vervet Project conducted in a 12,000-hectares private game reserve, "Mawana", in KwaZulu Natal, South Africa (S 28° 00.327; E 031° 12.348). The vegetation of the study site is classed as Savannah biome, characterized by areas of grasslands with dispersed singular or clusters of trees forming a mosaic with the typical savannah thornveld, bushveld and thicket patches and the home range sizes of our studied groups of vervet monkeys approximated 160 hectares (van de Waal et al. 2013b). The monkeys where totally wild before habituation started in 2010 and had only human contact with hunters and/or poachers within their territories. Experiments were mainly conducted in winter when food resources are scarce (documented in online material of van de Waal et al. 2013b), so monkeys were motivated to participate.

All participating monkeys lived in groups of 30 to 48 individuals, typically composed of a few adult males with many adult females and juveniles (detailed group composition in Table 1). The hierarchy within each group has been documented by field assistants on the basis of the outcomes of conflicts between pairs of individuals and priority of access to food sources. Rank is typically stable between adult female vervets and the males in each group, but there were some changes in the hierarchies during the study, with sub-adult females giving birth to their first infant and

entering the adult female hierarchy as well as some changes in the male hierarchy, often resulting from migrations.

All individuals were identified by their faces. A recognition file with portrait photographs and specific individual features (scars, colour, etc) was constructed for each group. Monkeys were named with letter codes. Matriline membership assignment was based on behavioural data: mothers nursing infants and adult females frequently being close to and tolerant of juveniles in feeding and resting contexts were taken as evidence for matriline membership.

Experimental procedures

The experimental apparatus was that used in our earlier studies with vervets in sanctuaries (van de Waal et al. 2013a) and consisted of an opaque plastic box, 10x10x10cm, with a door on one side that could be slid to either side or instead lifted up to access the contents (Fig.1a-b, video 1-2). The food reward inside was $1/20^{th}$ of an apple, that all monkeys were used to in other experimental settings and captures. The box thus acted as an 'artificial fruit' (Whiten et al. 1996), here called a 'vervetable', designed for testing the social learning of alternative opening techniques. The alternative opening methods resemble those of a 'doorian' fruit used in previous studies with chimpanzees (Horner et al. 2006) and capuchin monkeys (Dindo et al. 2008, 2009), but the slide door in the vervetable could additionally move to either side (whereas it was restricted to one side in the 'doorian') and was larger than that used in the capuchin study. Holes on the sides of the vervetable allowed it to be anchored to the ground using rope and camping hooks.

142 The experiments took place at sunrise close to a sleeping site. Experimental boxes (one
143 during demonstrations, four to eight during experimental phases) were anchored to the ground.
144 The spacing between the boxes was a minimum of half a meter and orientation was variable
145 depending on vegetation density and visibility. The experimental procedure began with a step-
146 wise training phase in which the individual most focused on the task could learn only one
147 opening solution (either lift, slide to the right or slide to the left) by trial-and-error because other
148 opening solutions were physically blocked through the tightening of appropriately-located bolts,
149 limiting opening to one technique in each group. Once an individual mastered the opening
150 technique it was allowed to perform over 50 openings ('demonstrations') and until a minimum of
151 half of the group observed the demonstration from a 5m radius of the box (AK group 54
152 demonstrations, 17 observers; BD group 71 demonstrations, 23 observers; NH group 70
153 demonstrations, 24 observers). Demonstrations took place over an average of 9 days (range 6-12)
154 with an average of 8 demonstrations per day (range 2-12), each time involving only a single
155 vervetable to ensure its exclusive access and performance of a specific opening technique,
156 alternative solutions remaining blocked. The remainder of the group were able to watch these
157 demonstrations. By fixing the number of demonstrations to at least 50 we ensured that a
158 minimum of 2/3 individuals of each group observed an opening at least once. Females were
159 preferred models, as van de Waal and colleagues (2010) found that in the wild, adult female
160 vervets are more likely to be watched and learned from than males. We first attempted to attract
161 the dominant female of each group as a model by presenting the baited box open, in proximity to
162 her. Where there was a lack of response, we trained the most food motivated and boldest adult

163 female of each group who approached the vervetable, namely Nkosikasi (4th in rank) in AK, Asis
164 (3rd in rank) in BD and Paris (4th in rank) in NH.

165 After the demonstration phase, an experimental phase consisted of 15 days in each of the
166 three groups, with up to eight vervetables offered at one time. The vervetables used during the
167 demonstration phase were also used during the experimental phase. We initially offered four
168 boxes but quickly decided to switch to eight as an optimal number to spread access across the
169 group while being able to monitor all boxes; in this, number of sessions and boxes was kept
170 comparable across all groups. We refer to each day of testing as a 'session', during which a
171 monkey might achieve one or several openings. All vervetables were unlocked so that any
172 technique could now be used. All monkeys were free to interact with the vervetables repeatedly
173 within the constraints of the social group dynamics, such as rank. As a result, the total number of
174 openings per monkey naturally varied. Once any ververtable was opened, an experimenter slowly
175 approached and re-baited it. All interactions with the vervetables were recorded using one video
176 camera during the demonstration phase and two during the experimental phase, because the latter
177 involved multiple vervetables to prevent monopolisation. The average duration of a
178 demonstration session was of 29 minutes and the average duration of an experimental session
179 was of 1hour 21min.

180 *Data coding, analyses and statistics*

181 For each manipulation of a vervetable we recorded which monkey performed it, which
182 technique was used (lift, slide to the right, slide to the left) and whether the monkey managed to
183 open the door successfully and gain the reward or not. Most openings were coded live in the

field, with the few openings that could not be followed during the experiment coded later from videos, concerning either the identity of the manipulating monkey or the opening technique. We found that all codings were unambiguous as they involved quite different manipulations of the apparatus (lift, slide right or left), and such measures were always taken by two coders (EW and one other staff member of IVP); inter-observer reliability was 100%.

We also coded the ID of each monkey who was less than 5m from a successful manipulation and attentive to the opener. The attention of these individuals was considered positive if the monkey was otherwise inactive and had its head orientated towards the manipulator. These data were coded in the field by EW and one other staff member of IVP; only if both observers had coded the monkey as attentive was it taken in account for the analyses.

We analysed the effects of monkeys observing 'lift' versus 'slide' techniques and 'slide right' versus 'slide left' techniques separately in terms of three principal hypotheses regarding social learning. First, we used R (R Core Team 2013) to perform two-tailed permutation tests with 10 000 permutations to test the prediction that the first successful technique used by each individual would be similar to the technique introduced into their group (whether because they learned from the model or another monkey). Second, focusing on the overall difference between groups' techniques, we used IBM SPSS Statistics 21.0 (SPSS Inc., Chicago, IL, U.S.A.) to create binomial Generalized Linear Models (GLM) with a logit link to test whether the behaviour of individuals in the different groups was predicted by the technique used by their initial models and to calculate the correlation between attention and actions used.

Ethics guidelines

We adhered to the "Guidelines for the Use of Animals in Research" of the Association for the Study of Animal Behaviour. Our experiments were approved by the relevant local authority, Ezemvelo KZN Wildlife, South Africa; by the funder, Swiss National Science Foundation and by the Ethics Committee of the School of Psychology & Neuroscience, University of St Andrews, UK. Our set-up involved potential opportunities for feeding competition. However, as we were mainly interested in individuals' first manipulation, we offered multiple test boxes, which minimised any conflict. We also kept the amount of food relatively small (1/20 of an apple in each trial) both in the demonstration and experimental phases.

RESULTS

Across all three groups, 49 out of 121 individuals approached the vervetable and touched the box ~~or the door~~. Seventeen individuals, out of 121 in the three groups, successfully opened a vervetable at least once. Only eight of the 32 unsuccessful manipulators touched the door during their manipulation. Excluding the models, it was mainly juveniles that successfully opened the apparatus (23% of adults and 77% of juveniles). We removed one individual from our analysis, 'Porto', as he interacted and successfully opened the apparatus during the demonstration phase, being tolerated by the model 'Paris', his mother; thus our sample size of successful openers, apart from the models, was 13. Individuals younger than one year old never participated in the experiments. Evidence for social learning was evaluated in the following three analyses (see ESM for data set).

226 *Testing for social learning: first successes*

227 On their first opening, 11 out of 13 group members adopted the technique their model had used.
228 We found that members of the 'slide' groups were significantly more likely to use 'slide' in their
229 first success than members of the 'lift' groups (Exact permutation test: N=13, p=0.038, Fig. 2).

230 The difference between the 'slide-left' and the 'slide-right' groups regarding the direction of
231 movement on first 'slide' success was not significant (Exact permutation test: N=6, p=0.4).
232 However, only six monkeys in the two slide groups, three per group, solved the vervetable (2
233 sliding to the right and 1 to the left in each group), limiting the power of the test.

234

235 *Testing for social learning: differences between groups across all trials*

236 To evaluate the strength of any socially learned differences between groups we fitted a GLM with
237 the number of successful 'lift' actions across all sessions relative to the total number of successes
238 for each individual as the dependent variable and the technique used by the model, either 'lift' or
239 'slide' as a single factor. We found that individuals who had been exposed to a model using 'lift'
240 were significantly more likely to use 'lift' than if the model had used 'slide' (Wald $\chi^2_1 = 28.28$,
241 N=13, P <0.001, Fig. 3).

242 We used the same technique to fit a GLM with the number of successful 'slide-right' actions
243 across all sessions relative to the total number of successful 'slide' actions for each individual as
244 the dependent variable and the technique used by the model, either 'lift', 'slide-right' or 'slide-
245 left' as a single factor. In this analysis, the group in which the models had been trained to perform

246 'lift' are used as a contrast because these models provided no information regarding the direction
247 in which the door could slide. We found that the technique demonstrated had a small but
248 significant main effect (Wald χ^2_2=6.35, *N*=13, *P*=0.042) but that the effect resulted from the fact
249 that individuals who had not been exposed to a model using 'slide' were more likely to use a
250 'slide-left' technique than individuals who had seen a 'slide-left' (Wald χ^2_1=3.84, *N*=8, *P*=0.050)
251 or a 'slide-right' model in their group (Wald χ^2_1=3.58, *N*=10, *P*=0.058). There was no significant
252 difference between 'slide-left' and 'slide-right' (Wald χ^2_1=1.36, *N*=8, *P*=0.24).

253

254 *Does the proportion of 'lift' versus 'slide' witnessed overall predict the option adopted?*

255 Building on approaches developed in a two-action social diffusion study in young children
256 (Whiten and Flynn 2010: compare Figures 3 and 4 therein), Figure 4 shows each successive
257 monkey's openings during their first successful session of 'lift' versus 'slide' actions before the
258 next monkey opened a vervetable, for each of the groups (Fig. 4a = Baie Dankie group, 4b=
259 Ankhase group, 4c= Noha group). Arrows indicate the putative direction of information flow,
260 because these arrows originate from each monkey that the focal individual had watched prior to
261 its first success, and the proportion of 'lift' versus 'slide' actions witnessed as a result is indicated
262 in each case. These data permitted us to address whether the proportion of 'lift' witnessed overall
263 predicted a corresponding bias in an individual's actions.

264 We found that the percentage of the 'lift' technique witnessed overall was significantly correlated
265 with the percentage of 'lift' that individuals used during their first successful session (Spearman

correlation, N=13, rho=0.76, P=0.003; Fig.5a) as well as to the percentage of 'lift' used during the whole experiment (Spearman correlation, N=13, rho=0.808, P=0.001, Fig.5b).

DISCUSSION

Our results provide evidence of social learning in wild vervet monkeys that discriminate between different ways to process an artificial fruit item. We observed matching of whichever of two alternative methods had been experimentally seeded in a participant's group, both in the first opening and in overall behaviour subsequently. Overall, there was a strong positive correlation between techniques witnessed by each individual and the technique they adopted. This latter result took into account occurrences when individuals sometimes saw techniques different to those seeded, and thereby permitted a finer-grain assessment of actions done in relation to those witnessed. Here we address three principal implications of our results.

1. Two-action tests in the wild

Field experiments remain rare, but already cover taxa ranging from fish to birds and suricates (Helfman and Schultz 1984; Langen 1996; Lefebvre 1986; Thornton and Malapert 2009; Warner 1988; for a review see Reader and Biro 2010). Such experiments on primates have only recently been completed, demonstrating social learning in the wild (lemurs: Kendal et al. 2010b; Schnoell et al. 2014; vervet monkeys: van de Waal et al. 2010; van de Waal and Bshary 2011; van de Waal et al. 2012; van de Waal et al. 2013b; van de Waal et al 2014; marmosets: Gunhold et al. 2014a, 2014b). However two-action experiments in wild primates remain even more uncommon: two on

lemurs (Kendal et al. 2010b; Schnoell and Fichtel 2012; Schnoell et al. 2014), two on marmosets (Gunhold et al. 2014a, 2014b) and one on vervet monkeys (van de Waal et al 2010), their designs limited in identifying the social learning mechanism implicated. As Schnoell and Fichtel (2012) in a study incorporating a door that could either be pulled or pushed according to where lemurs put their muzzles, acknowledge that: '…the exact learning mechanism could unfortunately not be determined with this experimental setting'. Kendal et al. (2010b) used a similar set-up. By contrast, in our study monkeys grasped the same knob on a door to perform either 'slide' or 'lift', so that the copying we observed was not explicable by local enhancement but rather concerned alternative movements, thus implicating either imitation or emulation We believe that our results and those recently reported for marmosets by Gunhold et al. (2014a) provide the first such evidence derived from two-action field experiments with wild primates.

2. Correlations between relative frequency seen and relative frequency done

Our detailed data on what each individual had been likely to see before it worked on our foraging task (Fig. 4) permitted computations of correlations that provide fine grain support of the link between observation and learning a new task. These findings are consistent with observational field evidence for primates suggesting vertical transmission, where tolerance and close observations allow juveniles to adopt their mother's foraging methods (Lonsdorf et al. 2004; Perry 2009; Jaeggi et al. 2010). Earlier, we have also shown experimentally that wild vervet monkeys display vertical social transmission in both food preference (van de Waal et al. 2013b) and food handling (van de Waal et al. 2014). These social learning responses may reflect

307 (a) conformity to the preference of a majority of several monkeys watched (Claidière and Whiten
308 2012); (b) matching the overall total frequency of actions witnessed (Perry 2009); or (c) matching
309 focussed on one key individual such as the mother (van de Waal et al. 2014) or a higher status
310 individual (Horner et al. 2010). We do not yet have enough data to discriminate such alternatives
311 for the task described here, but in many cases individuals watched only one or few others,
312 suggesting a conformity effect may be unlikely.

313

314 3. Minimal success across the group as a whole

315 The proportion of individuals in our groups who were successful in the study was low, at only
316 17 among 121 monkeys. As a result we cannot address the level of granularity in what was
317 learned compared to captive vervets in our earlier study who even copied whether the sliding of
318 the door was to the right or to the left (van de Waal et al. 2013a). What is responsible for the low
319 rates of participation and successful openings? One possibility is that it is linked to model
320 identities. All our models, determined by which individuals approached the task first, were adult
321 females ranked only 3rd or 4th in the female hierarchy. Van de Waal and colleagues (2010) found
322 selective attention of wild vervets towards dominant females and not towards dominant males in
323 another two-action test and hypothesised that the philopatric sex should be more copied in a
324 foraging task. However, natural observations of gaze during adult vervet monkeys' foraging
325 revealed that adult females are more observed than adult males, irrespectively of their rank
326 (Renevey et al. 2013). The question of whether greater participation would follow actions by
327 alpha females remains open and further investigations are needed.

We have described a field experiment demonstrating that wild primates may discriminate and copy alternative means for processing difficult food types, and tracked the initial progress of social information transfer within the group. These approaches should be applicable to many other species, and with sufficient sensitivity to the social dynamics of the groups concerned, offer prospects for deeper analyses of social learning in wild populations in the future.

Acknowledgements

This project was supported by a Sinergia grant (CRSI33_133040) from the Swiss National Science Foundation to R. Bshary, C. P. van Schaik and A. Whiten, and by a SNSF personal grant of E.W. (P300P3_151187). We are particularly grateful to Kerneels van der Walt for permission to conduct the study in his reserve and Albert Driescher for his vital support in the field. The study was registered with Ezemvelo KZN Wildlife in South Africa and gained approval from the Ethics Committee of the School of Psychology and Neuroscience, University of St Andrews. We are grateful to all IVP field team for assistance in data collection during experimental sessions. Thanks to Andy Burnley for constructing the vervetables. We are grateful to Tina Gunhold for useful comments on the manuscript.

REFERENCES

347 Aplin LM, Sheldon BC, Morand-Ferron J (2013) Milk bottles revisited: social learning and
348 individual variation in the blue tit, (*Cyanistes caeruleus*). Anim Behav 85:1225–1232. doi:
349 10.1016/j.anbehav.2013.03.009

350 Bugnyar T, Huber L (1997) Push or pull: an experimental study on marmosets. Anim Behav
351 54:817–831. doi: 10.1006/anbe.1996.0497

352 Claidière N, Whiten A (2012) Integrating the study of conformity and culture in humans and
353 nonhuman animals. Psychol Bull 138(1):126–145. doi: 10.1037/a0025868

354 Dawson BV, Foss BM (1965) Observational learning in budgerigars. Anim Behav 13:470–474.

355 Dindo M, Thierry B, Whiten A (2008) Social diffusion of novel foraging methods in brown
356 capuchin monkeys (*Cebus apella*). Proc R Soc B 275:187–193. doi: 10.1098/rspb.2007.1318

357 Dindo M, de Waal FBM, Whiten A (2009) In-group conformity sustains different foraging
358 traditions in capuchin monkeys (*Cebus apella*). PLoS One 4:e7858. doi:
359 10.1371/journal.pone.0007858

360 Galef BG Jr, Allen C (1995) A new model system for studying animal tradition. Anim Behav
361 50:705–717. doi: 10.1016/0003-3472(95)80131-6

362 Gunhold T, Massen JJM, Schiel N, Souto A & Bugnyar T (2014a) Memory, transmission and
363 persistence of alternative foraging techniques in wild common marmosets. Anim Behav
364 91:79–91. doi: 10.1016/j.anbehav.2014.02.023

365 Gunhold T, Whiten A, Bugnyar T (2014b) Video demonstrations seed alternative problem-
366 solving techniques in wild common marmosets. Biol Lett 10(9):20140439. doi:
367 10.1098/rsbl.2014.0439

368 Helfman GS, Schultz ET (1984) Social transmission of behavioural traditions in a coral reef fish.
369 Anim Behav 32:379–384

370 Hopper LM, Spiteri A, Lambeth SP, Schapiro SJ, Horner V, Whiten A (2007) Experimental
371 studies of traditions and underlying transmission processes in chimpanzees. Anim Behav
372 73:1021–1032. doi: 10.1016/j.anbehav.2006.07.016

373 Hoppitt W, Laland KN (2008) Social Processes influencing learning in animals: a review of the
374 evidence. Adv Stu Behav 38:105–165. doi: 10.1016/S0065-3454(08)00003-X

375 Horner V, Whiten A, Flynn EG, de Waal FBM (2006) Faithful replication of foraging techniques
376 along cultural transmission chains by chimpanzees and children. P Natl Acad Sci USA
377 103:13878–13883. doi: 10.1073/pnas.0606015103

378 Horner V, Proctor D, Bonnie KE, Whiten A, de Waal FBM (2010) Prestige affects cultural
379 learning in chimpanzees. PloS One 5(5):e10625. doi: 10.1371/journal.pone.0010625

380 Jaeggi AV, Dunkel LP, Van Noordwijk MA, Wich SA, Sura AA, van Schaik, CP (2010) Social
381 learning of diet and foraging skills by wild immature Bornean orangutans: implications for
382 culture. Am J Primatol 72(1):62–71. doi: 10.1002/ajp.20752

383 Kendal RL, Galef BG, van Schaik CP (2010a) Social learning research outside the laboratory:
384 How and why?. Learn Beha. 38:187–194. doi: 10.3758/LB.38.3.187

385 Kendal RL, Custance DM, Kendal JR, Vale G, Stoinski TS, Rakotomalala NL, Rasamimanana H
386 (2010b) Evidence for social learning in wild lemurs (*Lemur catta*). Learn Behav 38:220–234.
387 doi: 10.3758/LB.38.3.220

388 Langen TA (1996) Social learning of a novel foraging skill by white-throated magpie-jays
389 (*Calocitta formosa, Corvidae*): a field experiment. Ethology 102:157–166

390 Lefebvre L (1986) Cultural diffusion of a novel food-finding behaviour in urban pigeons: an
391 experimental field test. Ethology 71:295–304

392 Lonsdorf EV, Eberly LE, Pusey AE (2004) Sex differences in learning in chimpanzees. Nature
393 428(6984):715–716. doi: 10.1038/428715a

394 Nielsen M, Subiaul F, Galef BG Jr, Zentall, TR, Whiten A (2012) Social learning in humans and
395 non-humans animals: Theoretical and empirical dissections. (Introduction to special issue) J
396 Comp Psychol 126:109–113. doi: 10.1037/a0027758

397 Perry S (2009) Conformism in the food processing techniques of white-faced capuchin monkeys
398 (*Cebus capucinus*). Anim Cogn 12:705–716. doi: 10.1007/s10071-009-0230-3

399 R Core Team (2013) R: A language and environment for statistical computing. Vienna, Austria:
400 R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/

401 Reader SM, Biro D (2010) Experimental identification of social learning in wild animals. Learn
402 Behav 38(3):265–283. doi: 10.1016/j.evolhumbehav.2011.11.010

403 Renevey N, Bshary R, van de Waal E (2013) Philopatric vervet monkey females are the focus of
404 social attention rather independently of rank. Behaviour 150:599–615. doi:
405 10.1163/1568539X-00003072

406 Schnoell AV, Fichtel C (2012) Wild redfronted lemurs (*Eulemur rufifrons*) use social information
407 to learn new foraging techniques. Anim Cogn 15:505–516. doi: 10.1007/s10071-012-0477-y

408 Schnoell AV, Dittmann MT, Fichtel C (2014) Human-introduced long-term traditions in wild
409 redfronted lemurs?. Anim Cogn 17(1):45–54. doi: 10.1007/s10071-013-0636-9

410 Thornton A, Malapert A (2009) Experimental evidence for social transmission of food
411 acquisition techniques in wild meerkats. Anim Behav 78:255–264. doi:
412 10.1016/j.anbehav.2009.04.021)

413 Thornton A, Clutton-Brock T (2011) Social learning and the development of individual and
414 group behaviour in mammal societies. Phil Trans R Soc B 366:978–987. doi:
415 10.1098/rstb.2010.0312

416 Thorpe WH (1963) Learning and instinct in animals, 2nd edn. Methuen, London.

417 Tomasello M (1990) Cultural transmission in tool use and communicatory signalling of
418 chimpanzees. In: Parker S, Gibson K (eds) "Language" and intelligence in monkeys and apes:
419 Comparative developmental perspectives. Cambridge University Press, Cambridge, pp 274-
420 311.

421 Voelkl B, Huber L (2000) True imitation in marmosets. Anim Behav 60:195–202. doi:
422 10.1006/anbe.2000.1457

van de Waal E, Bshary R (2011) Social learning abilities of wild vervet monkeys in a two-step task artificial fruit experiment. Anim Behav 81:433–438. doi: 10.1016/j.anbehav.2010.11.013

van de Waal E, Whiten A (2012) Spontaneous emergence, imitation and spread of alternative foraging techniques among groups of vervet monkeys. PLoS One 7(10):e47008. doi: 10.1371/journal.pone.0047008

van de Waal E, Renevey N, Favre CM, Bshary R (2010) Selective attention to philopatric models causes directed social learning in wild vervet monkeys. Proc R Soc B 277:2105–2111. doi: 10.1098/rspb.2009.2260

van de Waal E, Krützen M, Hula J, Goudet J, Bshary B (2012) Similarity in food cleaning techniques within matrilines in wild vervet monkeys. PLoS One 7(4):e35694. doi: 10.1371/journal.pone.0035694

van de Waal E, Claidière N, Whiten A (2013a) Social learning and spread of alternative means of opening an artificial food in four groups of vervet monkeys (*Chlorocebus aethiops*). Anim Behav 85:71–76. doi: 10.1016/j.anbehav.2012.10.008

van de Waal E, Borgeaud C, Whiten A (2013b) Potent social learning and conformity shape a wild primate's foraging decisions. Science 340(6131):483–485. doi: 10.1126/science.1232769

van de Waal E, Bshary R & Whiten A (2014) Wild vervet monkey infants acquire the food-processing variants of their mothers. Anim Behav 90:41–45. doi: 10.1016/j.anbehav.2014.01.015

442 Warner RR (1988) Traditionality of mating site preferences in a coral reef fish. Nature 335:719–
443 721. doi: 10.1038/335719a0

444 Whiten A (1998) Imitation of the sequential structure of actions by chimpanzees (*Pan*
445 *troglodytes*). J Comp Psychol 112:270–281.

446 Whiten A, Ham R (1992) On the nature and evolution of imitation in the animal kingdom:
447 Reappraisal of a century of research. Adv Stud Behav 11:239–283.

448 Whiten A, Mesoudi A (2008) Establishing an experimental science of culture: animal social
449 diffusion experiments. Phil Trans R Soc B 363:3477–3488. doi: 10.1098/rstb.2008.0134

450 Whiten A, Flynn E (2010) The transmission and evolution of experimental microcultures in
451 groups of young children. Dev Psychol 46(6):1694–1709. doi: 10.1037/a0020786

452 Whiten A, Custance DM, Gomez JC, Teixidor P, Bard KA (1996) Imitative learning of artificial
453 fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). J Comp
454 Psychol 110:3–14. doi: 10.1037/0735-7036.110.1.3

455 Whiten A, Horner V, de Waal FBM (2005) Conformity to cultural norms of tool use in
456 Chimpanzees. Nature 437:737–740. doi: 10.1038/nature04047

457 Whiten A, Spiteri A, Horner V, Bonnie KE, Lambeth SP, Schapiro SJ, de Waal FBM (2007)
458 Transmission of multiple traditions within and between chimpanzee groups. Curr Biol
459 17:1038–1043. doi: 10.1016/j.cub.2007.05.031

460 Whiten A, Hinde RA, Laland KN, Stringer CB 2011 Culture evolves. (Introduction to whole
461 issue) Phil Trans R Soc B 366:938–948. doi: 0.1098/rstb.2010.0372

462 Wood D (1989) Social interaction as tutoring. In: Bornstein MH, Bruner JS (eds) Interaction in
463 human development. Hillsdale, NJ, Erlbaum, pp. 59-80

464 Zentall TR, Sutton JE, Sherburne LM (1996) True imitative learning in pigeons. Psychol Sci
465 7:343–46. doi: 10.1111/j.1467-9280.1996.tb00386.x

466 Zentall TR (2012) Perspectives on social learning in animals. J Comp Psychol 126:114–128. doi:
467 10.1037/a0025381

468

469 **Table legends:**

470 **Table 1** Group composition 2012-2013

471 Males (AM) were scored as adults once they migrated, while females (AF) were scored as adults
472 once they gave birth. Group members that did not fulfil these criteria were scored as juveniles
473 (JU). As some males migrated and some juvenile females gave birth during the study period, we
474 present here average numbers.

475

476 **Figure legends**

477 **Fig. 1** The 'vervetable': (a) door being lifted, (b) door being slid to right. For more illustrations of
478 vervetables, see [19] for the captive illustrations

479 **Fig. 2** Preferences for the technique used by the model on their first success: total number of
480 individuals using 'lift' or 'slide' on their first success in the groups seeded with a 'lift' or 'slide'
481 model (grey for 'slide' and white for 'lift')

482 **Fig. 3** Probability of performing 'lift' versus 'slide' across all sessions as a function of what the
483 model was trained to do (white for the one group with 'lift' model and grey for the two groups
484 with 'slide' model)

485 **Fig. 4** Inferred information flow through each group: a) group AK, b) group BD, c) group NH.
486 Each column represents one vervet (age class written above the name: adult, subadult, juvenile;
487 and sex as a symbol under the name ♀ = female, ♂ = male) and each row represents a session

488 day (numbered), with entries diagonally left to right expressing each individual's first opening
489 techniques on the relevant session: on left in white box, number of lifts; on right in grey box,
490 number of slides. The bold frame indicates the most common action in each case. Traced in
491 reverse, arrows track back to show whom an individual had been in a posture to observe before
492 starting to open vervetables, and the relative numbers of 'lift' versus 'slide' they had accordingly
493 apparently witnessed before their first successful opening, so arrow heads indicate inferred
494 information flow. Numbers across the bottom of the diagram show the total frequencies in the
495 whole series of sessions. Stars indicate whether the first action done was lift or slide.

496 **Fig 5** (a) Correlation between the percentage of the lift technique used during the session when a
497 monkey first successfully opened a vervetable and the percentage of lift actions that individuals
498 witnessed beforehand (b) Correlation between the percentage of lift technique used during the
499 whole experiment and the percentage of lift that individuals witnessed before their first success

500

501 **Video data**

502 **Video 1** Lift opening of the vervetable during demonstration phase (Baie Dankie group).

503 **Video 2** Slide to the right opening of the vervetable during demonstration phase (Ankhase
504 group).

505

506 **Table 1 :**

Group	AF	AM	JU	total
Ankhase	8	4	21	33
Baie Dankie	12	4	32	48
Noha	11	4	25	40
total	31	12	78	121

507

508 **Fig. 1**

509 a) b)

510

511

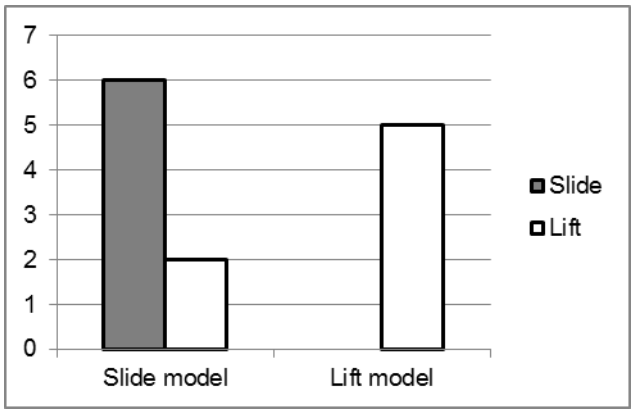
512

513

514

515

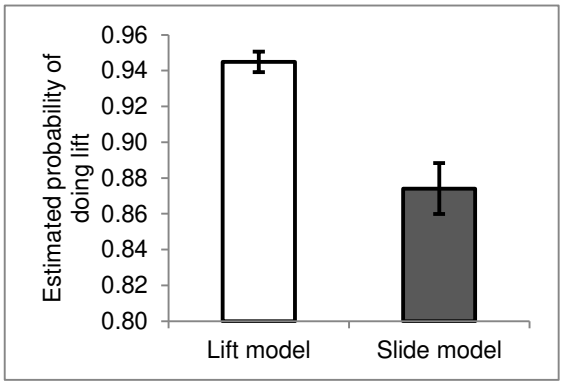
516 **Fig. 2**



517

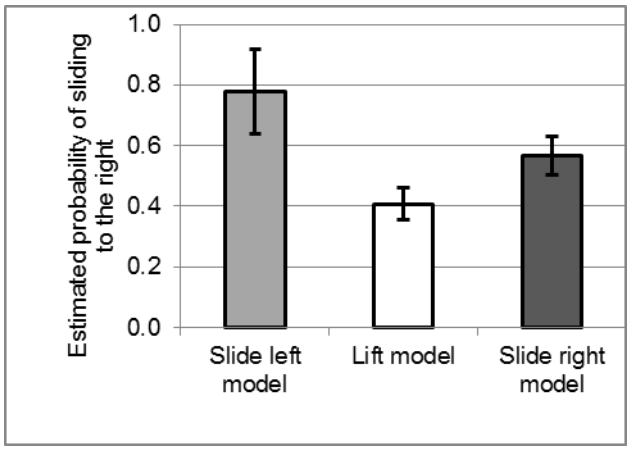
Fig. 3

a)



518

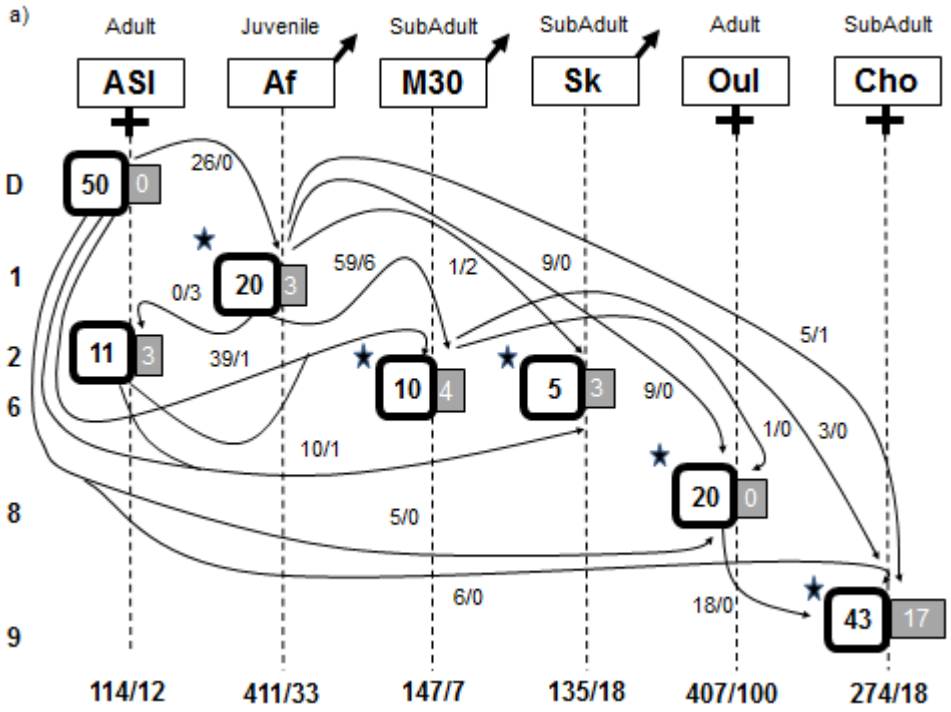
b)

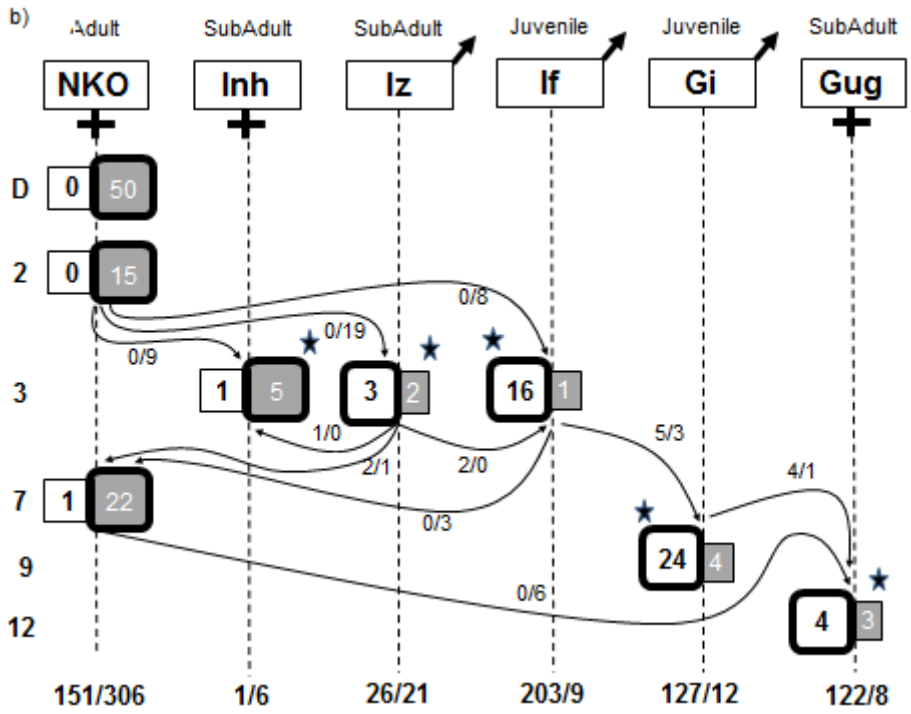


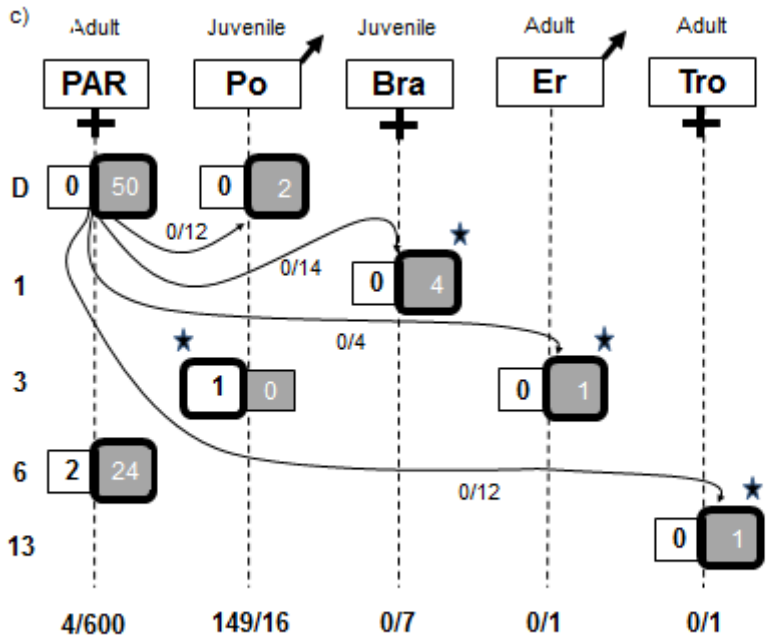
519

520

Fig. 4


a)
Adult
Juvenile
SubAdult
SubAdult
Adult
SubAdult
ASI
Af
M30
Sk
Oul
Cho
D
1
2
6
8
9
50
0
26/0
20
3
0/3
59/6
1/2
9/0
11
3
39/1
10
4
5
3
9/0
5/1
1/0
3/0
10/1
20
0
5/0
6/0
18/0
43
17
114/12
411/33
147/7
135/18
407/100
274/18

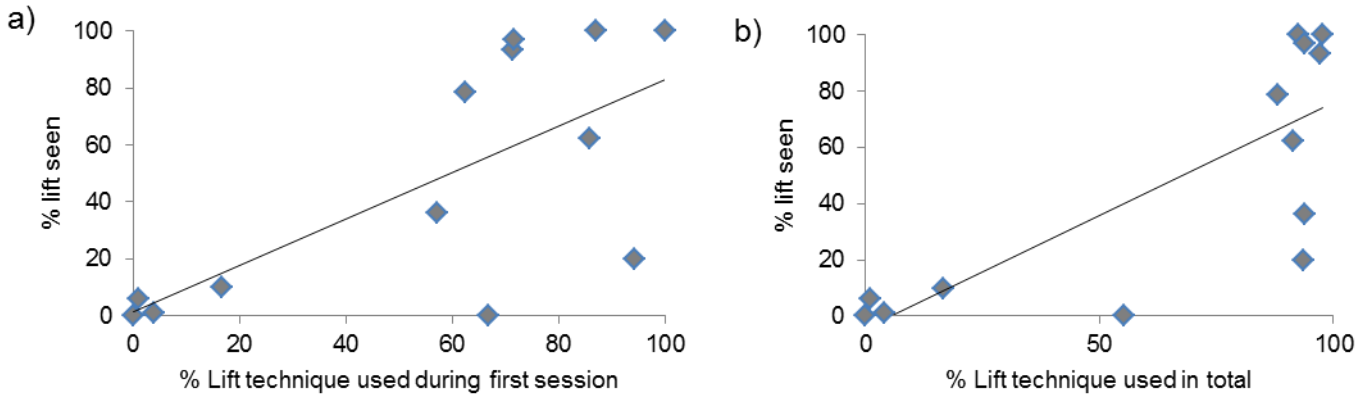

b)
Adult
SubAdult
SubAdult
Juvenile
Juvenile
SubAdult
NKO
Inh
Iz
If
Gi
Gug
D
2
3
7
9
12
0
50
0
15
0/8
0/19
0/9
1
5
3
2
16
1
1/0
5/3
2/1
2/0
4/1
1
22
0/3
24
4
0/6
4
3
151/306
1/6
26/21
203/9
127/12
122/8



525

526

Fig. 5



527